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Altitudinal Change in Plant Endemism, Species Turnover, and Diversity on Isla Santa Cruz, the Galápagos Islands[1]

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ABSTRACT: Vegetation zones of Isla Santa Cruz in the Galápagos Islands range from the lowland dry zone, through transition and moist zones, to the highland zone, reflecting the precipitation pattern. The zones are deflected upward on the leeward north side, as compared with the windward south side. The brown subzone and *Miconia robinsoniana* scrub of the moist zone are absent on the north side. Zonation and species distribution patterns are also related to altitude and substrate. Floristic and phytosociological endemisms for woody species increase with higher altitude, while those of herbaceous species are low in high elevations because of low endemism in pteridophytes. Species turnover rate along the altitudinal gradient is three times higher on the windward south side than on the leeward north side. Species diversity is low in *Scalesia pedunculata* forest, where stand-level dieback has occurred as a consequence of the species-poor constitution.

THE GALÁPAGOS ISLANDS are located on the equator in the eastern Pacific about 1000 km west of the South American coast. The islands are of volcanic origin, and the oldest lava is 3–4 million years old (Bailey 1976, Cox 1983). The highest peak is Volcan Wolf of Isla Isabela, 1707 m above sea level.

Regarding the vegetation ecology of the Galápagos Islands, Stewart (1911, 1915) was the first botanist who studied zonation; he described four vegetation zones: the dry, transition, moist, and grassy zones. He concluded that the zones were caused by differences in precipitation at different elevations on the islands. Similar views were presented by Bowman (1961), Fosberg (1967), Wiggins and Porter (1971), Itow (1971, 1990), Itow and Weber (1974), van der Werff (1978, 1979, 1980), and Hamann (1979, 1981), although the process and origin of treeless highland vegetation is somewhat controversial (see Stewart 1911, Wiggins and Porter 1971, Itow and Weber 1974, van der Werff 1978, Itow 1990).

Recent studies of zonation have focused on the island of Santa Cruz, which has well-differentiated vegetation zones and easily accessible study sites. Bowman (1961) clarified the zonation on the windward south side of this island, which ranges from the dry zone, through transition zone, *Scalesia* forest zone, brown zone and *Miconia* belt, to the upland zone, and gave elevational ranges of the zones (terminology here after Bowman 1961).

Fosberg (1967) reported the upward deflection of vegetation zones on the leeward north side of Santa Cruz, but did not refer to the actual elevations. Itow (1971) reported the elevational ranges of the zones on both the south and north sides and detected the absence of Bowman's brown zone and *Miconia* scrub on the north side, showing the upward deflection of the zones on the leeward slope.

The present paper describes zone differentiation and botanical characteristics of zones on both the south and north sides of Isla Santa Cruz, reconfirming and supplementing my earlier papers (Itow 1965, 1971, Itow and Weber 1974). The paper also deals with the altitudinal pattern of botanical endemism in

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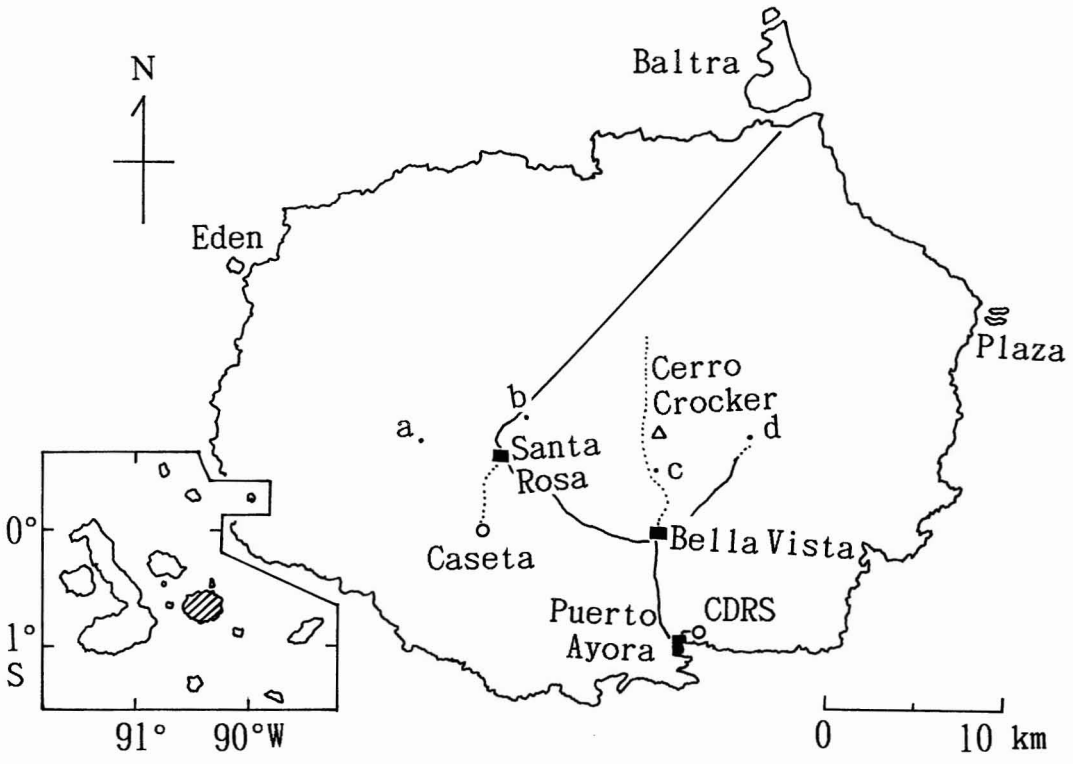

FIGURE 1. Map of the Galápagos Islands (*lower left*) and Isla Santa Cruz, showing the locations of field studies: a, Cerro Lechoso; b, Los Gemelos area; c, Cerro Media Luna; d, Cerro Mesa; CDRS, Charles Darwin Research Station.

the vegetation zones, and the species turnover and diversity of tree populations in relation to elevation on a single island.

Study Site

Isla Santa Cruz (Figure 1) is centrally located in the archipelago, between 0° 28′ 43″ S and 0° 46′ 23″ S and between 90° 10′ 05″ W and 90° 32′ 55″ W (Wiggins and Porter 1971). The island is a shield volcano of basaltic composition, with the highest point on the island being the summit of Cerro Crocker, 864 m above sea level. The topography is nearly flat to gently sloping at the lower elevations and becomes steeper at higher elevations. Several parasitic cinder cones are scattered in the middle and higher elevations. The topography of the summit area is irregular, and the central crater is not clearly defined.

The archipelago lies in the South Equatorial Current derived from the cold Humboldt Current and in the southeast trade wind zone. The air temperature is relatively cool and the precipitation is low for this equatorial location owing to the cool water of the Humboldt Current. The currents and winds control not only the weather and climate, but also the plant life in the islands.

The year is divided into two seasons: a warm season from January to May and a cool season from June to December. The weather is closely related to the action of the southeast trade winds that prevail in the Galápagos. In a normal year, the weak trade winds in the January–May period cause high temperatures and high precipitation at the low and middle elevations, especially on the windward south side of the islands. The strong trade winds in the June–December period bring cool air. In this season, precipitation is low at low elevations, taking the form of intermittent

drizzle, while the highlands, especially on the southern side of the island, are enveloped in clouds and fog during the daytime. The highlands receive considerable precipitation (Palmer and Pyle 1966, Wiggins and Porter 1971, Itow and Weber 1974, van der Werff 1978, Hamann 1979). Figure 2 illustrates three climate diagrams from different elevations on Isla Santa Cruz and one from Isla Baltra, which lies off the north coast of Santa Cruz. As seen from the Baltra diagram in comparison to the others, the leeward north side receives much less rainfall than the south side (Alpert 1963). The high precipitation in the highlands is largely in the form of fog drip and droplets condensed from moisture-saturated air (Itow and Weber 1974). The plant life is closely related to the distribution pattern of rainfall on both sides of the island and to the altitudinal gradient.

METHODS

Vegetation Sampling

Fieldwork was conducted in 1970, 1978, and 1981. Figure 1 shows the sites studied. The 1970 field trips took a route from the south coast up to the summit area of Cerro Crocker, up to the pass, west of Cerro Crocker, then down half the north side of the mountain. The Caseta area was also visited. The 1978 and 1981 field trips followed the road constructed in 1976 toward the north coast.

To sample the vegetation, in 1970 and 1978 I adopted the relevé method used by Braun-Blanquet (1964) and Mueller-Dombois and Ellenberg (1974), recording the vegetation height, cover abundance, and sociability of component species at each sample site. The topography, slope aspect, degree of slope steepness, and percentage of ground surface covered by unweathered lava were also recorded as habitat characteristics (Itow 1965, 1990).

In the 1978 and 1981 field studies of species

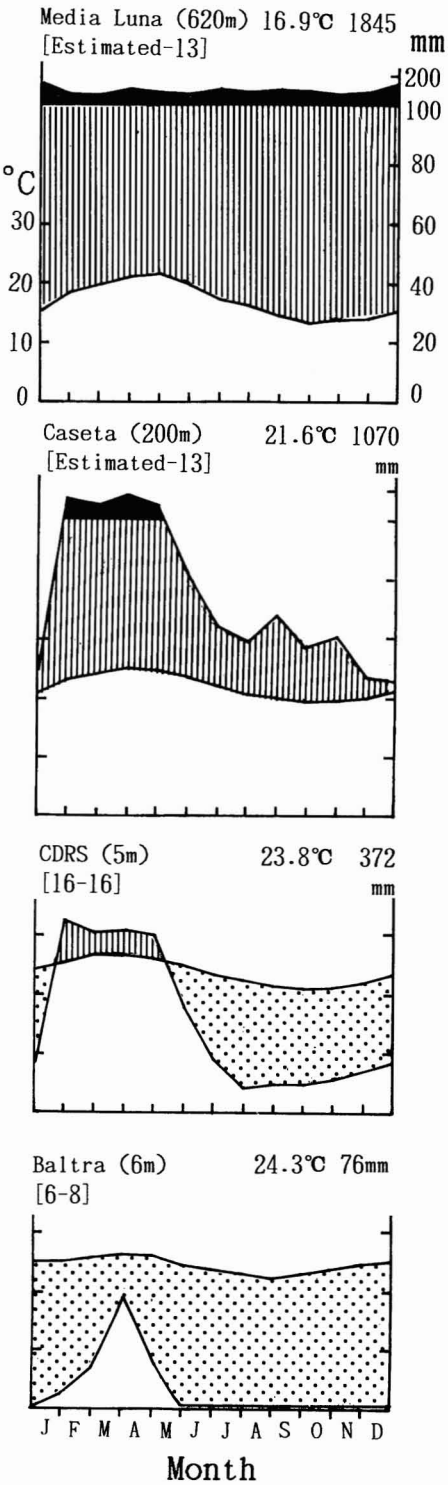

FIGURE 2. Climate diagrams for three different elevations on Santa Cruz, and for Baltra, off the north coast of Santa Cruz. ▷

turnover and botanical diversity, I adopted the minimum sampling program for tree populations (Itow 1984, 1988). It is a plotless sampling of more than 100 trees at each of the vegetation stands studied.

Voucher specimens were collected from plants that were thought critical, important, difficult in field identification, or new to the record. A set of duplicates of the 1970 collections is stored in the California Academy of Sciences Herbarium (CAS) and the rest are in the Nagasaki University Herbarium.

Processing of Data

FLORISTIC AND PHYTOSOCIOLOGICAL ENDEMISM. For the study of plant endemism and its pattern of distribution, I classified the relevés into eight groups: dry zone, transition zone, *Scalesia pedunculata* forest and *Miconia robinsoniana* scrub of the moist zone, and highland zone for the south side; and dry zone, transition zone, and *Scalesia* forest for the north side. The highland zone of the south side includes fens, bogs, and herbaceous and ericaceous communities (Itow and Weber 1974, Itow 1990). The phytosociological records of relevés were processed by the Braun-Blanquet method (1964) (Mueller-Dombois and Ellenberg 1974) in two-way tables for each of the eight relevé groups.

Two kinds of calculations were made of plant endemism: first, floristic endemism of each of the zones and second, phytosociological endemism of communities on each side of the island. This information was obtained by dividing the number of endemic species by the total number of species recorded in the zone or community. In calculating floristic endemism, the abundance and frequency of plants within the zone or community were not considered. To take the occurrence frequency of plants into consideration, phytosociological endemism was calculated for the zone or community. This information was obtained by dividing the cumulative number of records for endemic species in the zone by the cumulative number of records of all species in the same zone. An example of the calculation is as follows. Suppose two sites are sampled phytosociologically in a zone. At site 1, species A, B, C, D, e, f, g, and h are recorded, and at site 2, A, B, C, f, g, h, and i are recorded, where capital letters are endemics. (Usually the phytosociological record of each species consists of cover-abundance class and sociability class, or number of individuals [see Braun-Blanquet 1964, Mueller-Dombois and Ellenberg 1974], as in the present study.) The floristic endemism for that zone is obtained by dividing 4 (number of endemics) by 9 (number of all species recorded). For the same zone, the phytosociological endemism is obtained by dividing 7 (cumulative number of records for the four endemics in the two sample sites) by 15 (cumulative number of records for all the nine species) (in the present study, the cover-abundance and sociability classes and number of individuals were not taken into consideration). Phytosociological endemism is an indication of how often the endemics are encountered in the respective zones and communities.

TURNOVER OF SPECIES ALONG THE ALTITUDINAL GRADIENT. In the study of species turnover, the similarity among the sample sites (relevés) was calculated first. I adopted the Community Coefficient (Whittaker 1972) or Sorensen's Coefficient (Mueller-Dombois and Ellenberg 1974), $CC = 200c/a + b$, where a and b are the number of species found in site A and B, respectively, and c is the number of species common to both sites. In the present study, I calculated CC values only for tree and shrub species because the herbaceous flora and vegetation vary with, and depend on, the yearly fluctuation of weather conditions, especially rainfall in the growing season.

In calculating the species turnover rate along the altitudinal gradient, the procedure consisted of three steps (Itow 1989, 1991). The first step was the calculation of CC for every combination among the sample sites studied. The second step was to plot the calculated similarity values on a y axis (log scale) against the altitudinal difference on the x axis for each pair of relevés compared. The third step was the regression calculation through the plotted points. The slope of the regression line was the overall turnover rate of species per 1 m of altitudinal difference.

Extrapolation of the regression line to sea level (Wilson and Mohler 1983) gave the expected similarity of replicate samples, that is, the internal association (IA). The calculation procedure was basically similar to Whittaker's (1960, 1972) but differed in the use of the actual altitude for the x axis instead of his 10-segmented gradient. In the calculation of Half Change, however, I adopted Whittaker's (1960, 1972) method of $\beta = (\log a - \log z)/\log 2$, where a is IA and z is the similarity obtained by extrapolation of the regression line to the opposite end of the gradient. The regression calculations were done with the computer program presented by Tarumizu et al. (1984).

SPECIES DIVERSITY. In the study of species or alpha diversity, the present paper uses only the tree counts recorded by the minimum sampling program (Itow 1984, 1988). The tree counts in each sample site were processed using Hurlbert's (1971) index at 50 trees S_{50} (Itow 1984, 1988), Fisher's α (Williams 1947), and Shannon's H' (Pielou 1975), each of which shows alpha diversity levels.

RESULTS AND DISCUSSION

Vegetation Zonation

The pattern of vegetation distribution in the Galápagos Islands depends on two main factors, climate and substrate. Of the climatic factors, the amount of precipitation is of prime importance in the dry climate of the archipelago. Edaphically, different substrates such as lava, scoria and ash, and weathered soils constrain vegetation development and distribution.

In my preliminary vegetation study (Itow 1965), I described species and vegetation distribution in two-dimensional space, which consisted of percentage of ground covered by lava on the x axis and altitude on the y axis. The present study used the same gradient. Figure 3 illustrates the positions of sample sites in the above-mentioned x–y axes for the south and north sides of Santa Cruz. It also gives the ranges of six selected species and vegetation zones. Apparent differences between the south and north sides can be seen in the percentage of lava covering the ground surface. At low elevations, lava was little weathered on both sides, while in the middle elevations the lava was well weathered on the windward (i.e., wet) south side but poorly weathered on the leeward (i.e., dry) north side. This is clearly a reflection of the low rainfall on the leeward side and the consequent slow weathering of lava.

The combined effect of rainfall and weathering patterns results in the upward deflection of vegetation zones on the leeward side (Fosberg 1967) and the absence of the brown subzone and *Miconia robinsoniana* scrub on the same side (Itow 1971, Itow and Weber 1974). Table 1 gives the vegetation zonation on both sides as confirmed by fieldwork. The main criterion I adopted to discern the dry and transition zones was the presence of filamentous lichens on tree branches. Table 2 gives the constancy classes of component species recorded in my phytosociological relevés from the respective zones and communities on the south and north sides of Santa Cruz. The characteristics of the zones are summarized below. (Scientific names follow Wiggins and Porter [1971] and Porter [1979, 1983] for vascular plants and Weber [1966] for the two *Sphagnum* species. Asterisks (*) indicate species endemic to the Galápagos Islands.)

DRY ZONE. The vegetation is decidedly xerophytic, consisting of white-barked trees and shrubs such as *Bursera graveolens* (most common), *Croton scouleri** (narrow-leaved varieties), *Erythrina velutina*, *Piscidia carthagensis*, *Castela galapageia**, *Cordia lutea*, *Tournefortia pubescens**, and *Lantana peduncularis**. Some of them are drought-deciduous. Two giant cacti, *Opuntia echios** and *Jasminocereus thouarsii**, are prominent on the southern side (Figure 4, bottom left), but there are few on the northern side. The other plants restricted to the dry zone are thorny trees and shrubs of Leguminosae such as *Acacia macracantha*, *A. rorudiana**, *A. insulae-iacobi*, and *Parkinsonia aculeata*. In the endemic genus *Scalesia*, shrubby *S. affinis*

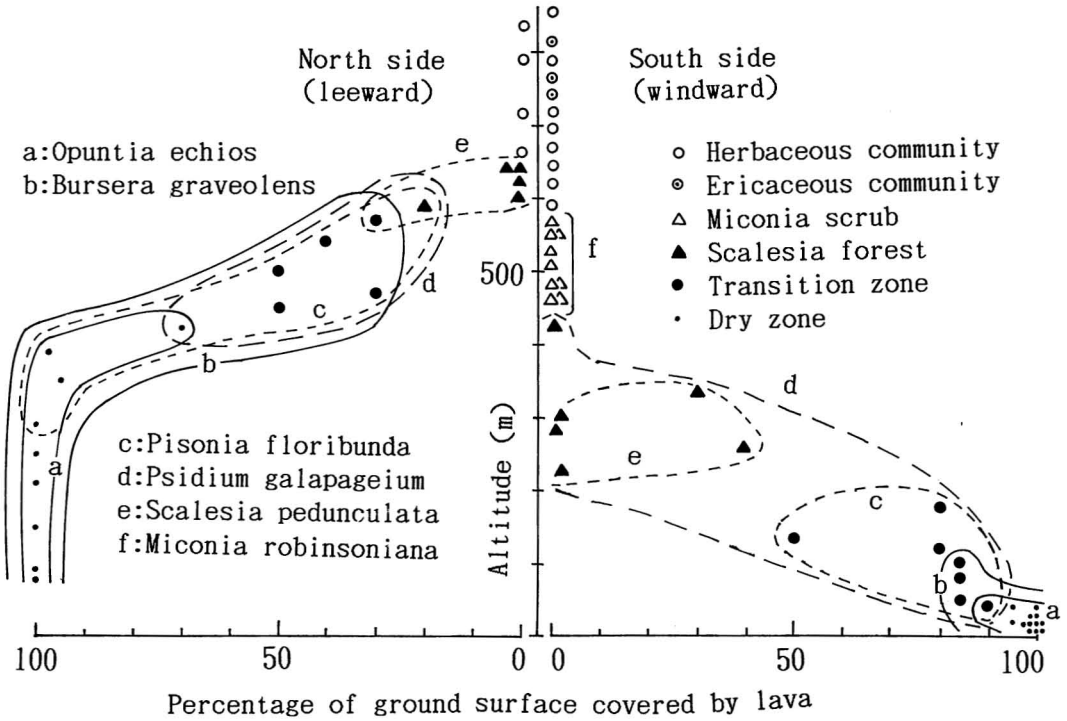

FIGURE 3. Distribution of sample sites in relation to the percentage of ground covered by lava and the altitude on the south and north sides. Six different symbols show sample sites from six different zones and communities. Lines and broken lines show the distributional ranges of a, *Opuntia echios*; b, *Bursera graveolens*; c, *Pisonia floribunda*; d, *Psidium galapageium*; e, *Scalesia pedunculata*; and f, *Miconia robinsoniana*.

TABLE 1

VEGETATION ZONES, THEIR ELEVATIONAL RANGES, AND PERCENTAGES OF GROUND COVERED BY LAVA ON THE SOUTH (WINDWARD) AND NORTH (LEEWARD) SIDES OF ISLA SANTA CRUZ, THE GALÁPAGOS ISLANDS

	SOUTH SIDE			NORTH SIDE		
VEGETATION ZONE	ELEVATIONAL RANGE (m)	PERCENTAGE OF LAVA (AVERAGE)	(RANGE)	ELEVATIONAL RANGE (m)	PERCENTAGE OF LAVA (AVERAGE)	(RANGE)
Dry zone	0–40	99	95–100	0–430	95	70–100
Transition zone	40–180	65	50–90	430–560	40	30–50
Moist zone						
Scalesia forest	180–280	12	0–40	560–670	5	0–20
Brown subzone	280–420	?	?	Absent		
Miconia scrub	420–580	0	0	Absent		
Highland zone	580–860	0	0	670–860	0	0

is restricted to the south side and shrubby *S. crockerii* to the north side. *Meytenus octogona* and *Scutia pauciflora* are also dry-zone shrubs. The absence of terrestrial and epiphytic ferns is one of the characteristics of the dry-zone vegetation. The coloration of the vegetated dry-zone landscape in the cool season is white to gray (Figure 4, bottom right)

TABLE 2

Floristic Composition of Vegetation Zones and Communities on the South and North Sides of Santa Cruz

	SOUTH SIDE					NORTH SIDE		
ZONE/COMMUNITY	A	B	C	D	E	A	B	C
NO. OF RELEVÉS	13	6	6	9	127	10	7	5
Woody endemics								
Acacia rorudiana	IV	·	·	·	·	·	·	·
Jasminocereus thouarsii	III	·	·	·	·	·	·	·
Lycium minimum	I	·	·	·	·	·	·	·
Scalesia affinis	I	·	·	·	·	·	·	·
Scalesia crockerii	·	·	·	·	·	II	·	·
Gossypium barbadense var. *darwinii*	·	·	·	·	·	II	·	·
Croton scouleri (narrow-leaved varieties)	III	·	·	·	·	III	·	·
Cordia anderssonii + *leucophlyctis*	II	·	·	·	·	III	I	II
Lantana peduncularis	I	·	·	·	·	II	III	I
Opuntia echios	V	III	·	·	·	IV	I	·
Castela galapageia	V	I	·	·	·	III	I	·
Tournefortia pubescens	III	II	·	·	·	III	IV	·
Pisonia floribunda	II	V	III	·	·	III	V	II
Croton scouleri var. *grandifolius*	·	V	·	·	·	·	·	·
Psidium galapageium	·	V	IV	·	·	I	V	III
Scalesia pedunculata	·	I	V	·	·	·	I	V
Tournefortia rufo-sericea	·	V	V	I	r	·	III	V
Psychotria rufipes	·	I	V	III	r	·	I	V
Pleuropetalum darwinii	·	·	I	I	·	·	·	·
Darwiniothamnus tenuifolius	·	·	·	I	·	·	·	I
Acnistus ellipticus	·	·	I	I	r	·	·	IV
Miconia robinsoniana	·	·	·	IV	r	·	·	·
Pernettya howellii	·	·	·	·	II	·	·	·
Cyathea weatherbyana	·	·	·	·	r	·	·	·
Borreria dispersa	·	·	·	·	r	·	·	·
Herbaceous endemics								
Alternanthera filifolia	II	·	·	·	·	·	·	·
Passiflora foetida var. *galapagensis*	I	·	·	·	·	·	·	·
Tiquilia sp.	I	·	·	·	·	·	·	·
Sarcostemma angustissima	I	·	·	·	·	II	·	·
Lycopersicon cheesmanii	·	·	·	·	·	I	·	·
Abutilon depauperatum	·	I	·	·	·	III	III	·
Acalypha paruvula + spp.	·	·	·	·	·	II	III	·
Alternanthera snodgrassii	·	·	·	·	·	III	I	I
Peperomia galapagensis	·	II	V	·	·	·	I	IV
Polypodium insularum	·	II	I	·	·	·	·	·
Asplenium formosum var. *carolinum*	·	II	II	·	·	·	I	IV
Passiflora colinvauxii	·	·	III	·	·	·	I	III
Peperomia petiolata	·	·	II	·	·	·	·	·
Tillandsia insularis	·	·	II	·	·	·	I	III
Pilea baurii	·	·	II	·	I	·	·	II
Phoradendron henslovii	·	·	I	·	·	·	·	II
Epidendrum spicatum	·	·	I	·	·	·	·	IV
Justicia galapagana	·	II	V	I	I	·	·	IV
Ctenitis pleiosoros	·	·	·	I	r	·	·	I
Jaegeria gracilis	·	·	·	·	I	·	·	·
Polypodium tridens	·	·	·	·	I	·	·	·
Paspalum galapageium	·	·	·	·	r	·	·	·
Drymaria monticola	·	·	·	·	r	·	·	·
Cyperus grandifolius	·	·	·	·	r	·	·	·
Polygonum galapagense	·	·	·	·	r	·	·	·
Hydrocotyle galapagensis	·	·	·	·	r	·	·	·

TABLE 2 (continued)

	SOUTH SIDE					NORTH SIDE		
ZONE/COMMUNITY	A	B	C	D	E	A	B	C
NO. OF RELEVÉS	13	6	6	9	127	10	7	5
Woody nonendemics								
Piscidia carthagensis	II	·	·	·	·	III	II	·
Scutia pauciflora	V	I	·	·	·	II	·	·
Bursera graveolens	IV	III	·	·	·	V	V	·
Erythrina velutina	II	I	·	·	·	II	·	·
Tournefortia psilostachya	III	IV	II	·	·	III	V	·
Chiococca alba	I	V	IV	·	·	IV	III	IV
Zanthoxylum fagara	II	V	V	I	r	IV	V	V
Herbaceous nonendemics								
Commicarpus tuberosus	IV	II	·	·	·	III	V	·
Trachypteris pinnata	II	IV	·	·	·	·	·	·
Plumbago scandens	I	III	II	·	·	II	II	I
Alternanthera halimifolia	·	V	V	·	r	·	I	V
Doryopteris pedata	·	I	V	I	·	·	·	IV
Asplenium cristatum	·	·	IV	·	·	·	·	II
Ctenitis sloanei	·	·	III	III	·	·	·	III
Pteridium aquilinum	·	·	·	III	IV	·	·	·
Hypericum uliginosum	·	·	·	·	III	·	·	·
No. of nonendemic species omitted	19	15	32	14	61	20	18	25

NOTE: Six constancy classes: V, 80–100%; IV, 60–80%; III, 40–60%; II, 20–40%; I, 5–20%; r, up to 5%. The endemics recorded in relevés are all listed; nonendemics are selected. A, dry zone; B, transition zone; C, *Scalesia pedunculata* forest; D, *Miconia robinsoniana* scrub; E, highland zone.

because of white-barked trees and shrubs. The surface of the substrate is nearly completely covered by unweathered lava blocks with little accumulation of organic material in which plants can root.

TRANSITION ZONE. This zone is literally transitional from xerophytic to mesophytic and the change is gradual (Reeder and Riechert 1975). The surface of the substrate consists of lava blocks and weathered soil. Vegetation of the lower half is made up mostly of dry-zone plants. *Bursera graveolens* trees reach a good size, up to 10 m in height, and cacti almost disappear. The undergrowth of the forests is much denser than in the dry zone. Ferns begin to occur in the ground layer of the forests and on tree trunks; the terrestrial fern *Trachypteris pinnata* is characteristic of this zone. In the upper half of the zone, vegetation is composed of fewer xerophytes and more mesophytes. An arborescent species of Compositae, *Scalesia pedunculata**, can be seen infrequently above the middle of the transition zone, but *Scalesia* trees reach their maximum size in the moist zone. Trees of *Psidium galapageium** and *Pisonia floribunda** also appear in this zone. One of the characteristics of this zone is the abundant growth of filamentous lichens (*Ramalina usnea* and *Usnea* species) on tree branches (Figure 4, center left).

MOIST ZONE. The mesophytic moist-zone vegetation can be divided into three subzones. They are *Scalesia pedunculata** forest belt, brown subzone (Bowman 1961), and *Miconia robinsoniana** scrub, of which the last two are absent on the north side of Santa Cruz (Figure 5) (Itow 1971).

The *Scalesia* forest is 8 to 12 m high and nearly monodominant (Figure 4, center right); associated species are represented by scattered trees of *Psidium galapageium** and *Pisonia floribunda**. The undergrowth is abundant, consisting of evergreen shrubs such as *Acnistus ellipticus**, *Psychotria rufipes**, *Tournefortia rufo-sericea**, *Croton*

FIGURE 4. Photographs of vegetation and communities on Isla Santa Cruz. *Bottom left*, dry-zone landscape around Charles Darwin Research Station on the windward south side of Santa Cruz; *bottom right*, dry-zone landscape in the cool (dry) season on the leeward north side, as seen from the summit of Isla Eden; *center left*, filamentous lichens on tree branches in transition zone on the south side; *center right*, *Scalesia pedunculata* forest at Los Gemelos area in moist zone; *top left*, *Miconia robinsoniana* scrub at the upper end of moist zone; *top right*, highland-zone landscape, as seen from the highest point of Cerro Crocker, with cinder cone (right arrow) and a small bog formation (left arrow, white in color) in a crater.

scouleri var. *grandifolius**, and *Chiococca alba* and also many ground-rooted ferns. Vascular plant epiphytes (ferns, orchids, and *Peperomia* spp.) and epiphytic bryophytes are also abundant.

The brown subzone was named for the abundant growth of brown liverworts (mostly *Frullania* species) that festoon branches of *Psidium galapageium** (Bowman 1961). The primary vegetation was already destroyed before 1964 and its identity is uncertain. This paper does not offer any phytosocio-

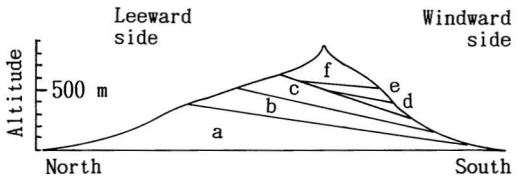

FIGURE 5. Schematic illustration of the vegetation zonation, showing the upward deflection on the leeward north side of Santa Cruz. a, dry zone; b, transition zone; c, *Scalesia* forest; d, brown subzone; e, *Misconia* scrub; f, highland zone.

logical and ecological data for the brown subzone.

The *Miconia* scrub is 2–3 m high and nearly monodominant (Figure 4, top left). The shrub has leathery leaves coated with thick cuticle. The stems and branches are covered by epiphytic mosses and ferns.

HIGHLAND ZONE. Treeless vegetation characterizes the highland zone, with ferns such as *Pteridium aquilinum*, *Blechnum polypodioides*, and *Nephrolepis cordifolia* and sedges such as *Rhynchospora rugosa* and *Scleria hirtella* being so prominent that the zone has been referred to as the fern-sedge zone (Wiggins and Porter 1971). The zone is heterogeneous and includes fens, raised bogs, and vertical bogs as well as herbaceous and ericaceous communities (Itow and Weber 1974, van der Werff 1978, Hamann 1981, Itow 1990).

Botanical Endemism

The overall endemism of the Galápagos vascular plant flora, from which gymnosperms are absent, is 7% in pteridophytes and 51% in angiosperms, excluding recently introduced species (Wiggins and Porter 1971, Porter 1979). Some of the indigenous plants, either endemic or nonendemic, were found nearly exclusively in a single vegetation zone (e.g., *Castela galapageia** in the dry zone and *Psychotria rufipes** in the moist zone), while others were seen in two or three neighboring zones (e.g., *Pisonia floribunda** in the dry, transition, and moist zones) (see Table 2).

Table 3 summarizes the number of woody and herbaceous species, and the number of endemics phytosociologically recorded in the respective zones and communities on both the south and north sides. A general trend in distribution of species number is that the number of woody species decreased from the dry to the highland zone while the number of herbaceous species, including pteridophytes, increased in the same direction with an exceptional small number at *Miconia* scrub. The number of woody endemics is fairly constant throughout the zones and communities and, therefore, the percentage endemism among the woody plants increased with elevation, of which an endemic tree fern, *Cyathea weatherbyana**, is included in the highland flora.

Regarding the herbaceous species recorded from the south side (Table 3), the number of pteridophyte species increased with elevation and the endemism among the herbaceous species decreased. This is because the mesophytic herbaceous plants include many pteridophytes (van der Werff 1990) and endemism among the pteridophytic flora is low. The total endemism calculated for all recorded species shows a decreasing trend from the dry to the highland zone on the south side, as has been pointed out also by Johnson and Raven (1973) and Porter (1979). On the north side, the number of pteridophyte species also increased with elevation, but the trend in herbaceous endemism was not clear.

The phytosociological endemism (Table 4) shows how often endemic species were encountered in vegetation sampling, reflecting the occurrence frequency of component species. Table 5 and Figure 6 show the pattern of phytosociological endemism on both the south and north sides of Santa Cruz. The phytosociological endemism of woody species increased with elevation on the south and north sides, reaching 64 and 74%, respectively, in the *Scalesia* forest of both sides and more than 90% in the *Miconia* scrub and highland on the south side (Table 4). The high phytosociological endemism in woody species is a reflection of the monodominance (see Diversity section) and high constancy values (Table 2) of woody endemics in the *Scalesia* forest and *Miconia* scrub as well as a high floristic endemism in the highland zone (Table

TABLE 3

FLORISTIC ENDEMISM (%) OF WOODY AND HERBACEOUS PLANTS IN DIFFERENT VEGETATION ZONES ON THE SOUTH AND NORTH SIDES OF SANTA CRUZ. HERBACEOUS PLANTS OF THE HIGHLAND ZONE INCLUDE TWO *Sphagnum* SPECIES

ZONE	DRY ZONE	TRANSITION ZONE	MOIST ZONE		HIGHLAND ZONE
COMMUNITY	*Bursera/ Opuntia*	*Bursera/ Pisonia*	*Scalesia pedunculata*	*Miconia robinsoniana*	FEN, BOG, HERBACEOUS, ERICACEOUS
South side					
Number of woody species	29	20	12	7	9
Number of woody endemics	11	9	7	6	7
Endemism (%)	38	45	58	86	78
Number of herbaceous species	15	20	45	19	72
(pteridophytes included)	(1)	(5)	(19)	(15)	(22)
Number of herbaceous endemics	4	5	10	2	10
(pteridophytes included)	(0)	(2)	(2)	(1)	(2)
Endemism (%)	27	25	22	11	14
Number of woody + herbaceous	44	40	57	26	81
Number of endemics	15	14	17	8	16
Endemism (%)	34	35	30	31	20

North side

ZONE	DRY ZONE	TRANSITION ZONE	MOIST ZONE
COMMUNITY	*Bursera*	*Bursera/ Pisonia*	*Scalesia pedunculata*
Number of woody species	23	20	12
Number of woody endemics	10	10	9
Endemism (%)	43	50	75
Number of herbaceous species	21	23	39
(pteridophytes included)	(0)	(2)	(10)
Number of herbaceous endemics	5	7	10
(pteridophytes included)	(0)	(1)	(2)
Endemism (%)	24	30	23
Number of woody + herbaceous	44	43	51
Number of endemics	15	17	19
Endemism (%)	34	40	37

3). The phytosociological endemism of herbaceous species was low in the *Miconia* scrub (7%) and highland zone (6%) on the south side, but that on the north side did not show a clear trend. Endemism trends in herbaceous species, either floristic or phytosociological, may change from year to year, depending on rainfall fluctuations that affect the germination and growth of annual and perennial herbaceous plants. This effect will be great in the dry zone where a number of nonendemic herbaceous plants appear in rainy years.

Species Turnover

As shown in Table 2, the species composition of plants in a vegetation zone changes toward the next zone. In the present study, the changing pattern of tree species was examined along the altitudinal gradient, using similarity

TABLE 4

PHYTOSOCIOLOGICAL ENDEMISM (%) OF WOODY AND HERBACEOUS PLANTS IN DIFFERENT VEGETATION ZONES ON THE SOUTH AND NORTH SIDES OF SANTA CRUZ. HERBACEOUS PLANTS OF THE HIGHLAND ZONE INCLUDE TWO *Sphagnum* SPECIES

ZONE / COMMUNITY	DRY ZONE *Bursera/ Opuntia*	TRANSITION ZONE *Bursera/ Pisonia*	MOIST ZONE *Scalesia pedunculata*	MOIST ZONE *Miconia robinsoniana*	HIGHLAND ZONE FEN, BOG, HERBACEOUS, ERICACEOUS
South side					
Cumulative no. of records for woody species	146	62	42	16	43
Cumulative no. of records for woody endemics	67	31	27	15	40
Endemism (%)	46	50	64	94	93
Cumulative no. of records for herbaceous species	50	42	92	61	770
(pteridophytes included)	(3)	(10)	(38)	(53)	(355)
Cumulative no. of records for herbaceous species	8	9	25	4	46
(pteridophytes included)	(0)	(4)	(3)	(1)	(15)
Endemism (%)	16	21	27	7	6
Cumulative no. of records for all species	196	104	134	77	813
Cumulative no. of records for all endemics	75	40	52	19	86
Endemism (%)	38	38	39	25	11

ZONE / COMMUNITY	DRY ZONE *Bursera*	TRANSITION ZONE *Bursera/ Pisonia*	MOIST ZONE *Scalesia pedunculata*
North side			
Cumulative no. of records for woody species	118	64	38
Cumulative no. of records for woody endemics	46	30	28
Endemism (%)	39	47	74
Cumulative no. of records for herbaceous species	55	61	87
(pteridophytes included)	(0)	(2)	(30)
Cumulative no. of records for herbaceous endemics	18	12	26
(pteridophytes included)	(0)	(1)	(7)
Endemism (%)	33	20	30
Cumulative no. of records for all species	173	125	125
Cumulative no. of records for all endemics	64	42	54
Endemism (%)	37	34	43

TABLE 5

NUMBER OF TREES (dbh >3 cm) SAMPLED BY THE MINIMUM SAMPLING PROGRAM, AND DIVERSITY MEASUREMENTS IN THE DRY AND TRANSITION ZONES ON THE WINDWARD SOUTH SIDE OF SANTA CRUZ

ZONE	DRY ZONE			TRANSITION ZONE			
SAMPLE SITE NO.	(1)	(2)	(3)	(4)	(5)	(6)	(7)
ALTITUDE (m)	10	15	15	50	90	110	140
*Jasminocereus thouarsii**	13	0	0	0	0	0	0
Maytenus octogona	6	0	0	0	0	0	0
*Cordia anderssonii**	2	0	0	0	0	0	0
*Opuntia echios**	50	51	48	16	3	1	0
*Croton scouleri** (narrow-leaved forms)	24	10	4	3	0	0	0
*Castela galapageia**	5	0	2	2	0	0	0
Acacia macracantha	5	7	7	5	5	2	0
Bursera graveolens	1	5	8	4	3	0	0
*Tournefortia pubescens**	2	2	0	7	0	0	0
Cordia lutea	1	2	1	1	0	0	0
Chiococca alba	1	2	3	5	7	2	6
Piscidia carthagensis	0	13	7	13	14	16	10
Zanthoxylum fagara	0	6	10	23	24	29	49
Parkinsonia aculeata	0	2	0	0	0	0	0
*Pisonia floribunda**	0	0	6	17	34	29	9
Erythrina velutina	0	0	4	2	0	0	0
*Tournefortia rufo-sericea**	0	0	0	1	3	1	2
Scutia pauciflora	0	0	0	1	0	0	0
*Psidium galapageium**	0	0	0	1	5	13	25
Croton scouleri var. *grandifolius**	0	0	0	0	4	8	1
Acacia insulae-iacobi	0	0	0	0	1	0	0
Tournefortia psilostachya	0	0	0	1	0	1	1
*Scalesia pedunculata**	0	0	0	0	0	1	0
Number of trees	110	100	100	102	103	103	103
Number of species	11	10	11	16	11	11	8
S_{50}	8.7	9.0	10.0	12.7	9.9	8.4	6.7
Fisher's α	3.0	2.8	3.2	5.3	3.1	3.1	2.0
Shannon's H'	2.4	2.4	2.6	3.3	2.8	2.6	2.1

NOTE: Asterisks indicate endemics.

values calculated from the Community Coefficient. (Herbaceous species were excluded from the calculation because of their yearly fluctuation due to rainfall.) The sample sites on the south side were from the dry and transition zones, while those on the north side were from those two zones plus the *Scalesia* forest. The similarity between sample sites (*CC* values) fell to zero from the dry zone to the *Scalesia* forest, indicating that no species were common to both sites. In plotting the *CC* values against the altitudinal difference (Figure 7), low similarities (ca. 12–14%) were found between sample sites whose altitudinal difference was more than 150 m on the south side and 400 m on the north side. The plotted points were nearly linear up to those altitudes. The regressions through them and the extrapolations to 0 m altitudinal difference gave the relationships of $\log Y = 1.97 - 0.0039X$ ($r = -0.76$; $P < 0.1$) for the south side and $\log Y = 1.96 - 0.0013X$ ($r = -0.83$; $P < 0.1$) for the north side, where X is the altitudinal difference in meters and Y is the similarity values in *CC*. In the equations above, the first parameter is the log value of internal association (IA) of replicate samples, and the second is the species turnover rate along the altitudinal gradient (Itow 1989, 1991).

Fosberg (1967) described the upward de-

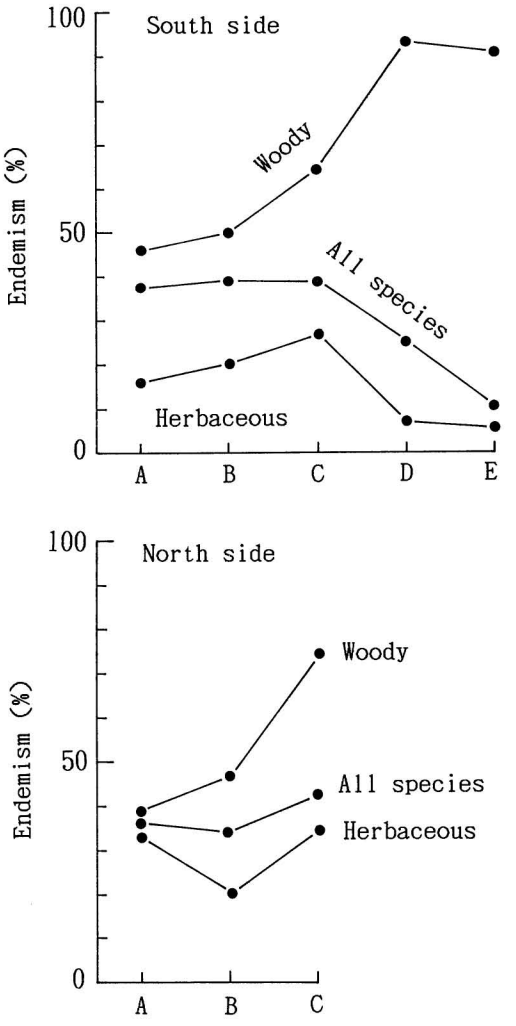

FIGURE 6. Patterns of phytosociological endemism (%) of woody, herbaceous (including ferns and allies, and two *Sphagnum* spp.), and all plant species on the south and north sides of Santa Cruz. A, dry zone; B, transition zone; C, *Scalesia pedunculata* forest; D, *Miconia robinsoniana* scrub; E, highland zone.

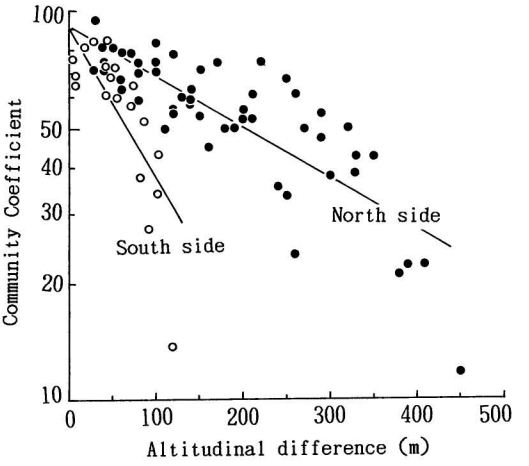

FIGURE 7. Relationships between similarity in *CC* and altitudinal difference on the south and north sides of Santa Cruz. Regressions are log $Y = 1.97 - 0.0039X$ for the south side and log $Y = 1.96 - 0.0013X$ for the north side. Internal association (IA) are 93.3 and 91.2 for the respective sides.

flection of vegetation zones on the leeward north side of Santa Cruz (cf. Figure 5). As shown in Table 1, the elevation of the moist zone is 3.2 times higher on the north side (which was 580 m above sea level) than on the south side (180 m). This means that the species distribution ranges along the altitudinal gradient are three times greater on the north side than on the south side. The slope of the two regression lines, -0.0039 for the south side and -0.0013 for the north side, showed clearly the expanded pattern of plant distributions on the north side, and coincided well with the upward deflection of the zones detected by Fosberg (1967). In the sense of Whittaker's (1972) beta diversity, the Half Change value (HC) up to the boundary of the transition and moist zones was 2.38 for the south side up to 180 m altitude and 2.43 for the north side up to 560 m.

Species Diversity and Scalesia *Forest Die-Back*

The Galápagos forests are poor in numbers of species for their equatorial location, especially when compared with the nearby Ecuadorian mainland or other continental forests (Itow 1988). In the present study, the diversity trend and pattern were studied along the altitudinal gradient. Tables 5 and 6 give the diversity measurements and calculations for the south and north sides, respectively.

Figure 8 illustrates the pattern of H' values along the altitudinal gradient. On the north (leeward) side, the trend was a slightly increasing one from the dry zone to the upper

TABLE 6

NUMBER OF TREES (dbh > 3 cm) SAMPLED BY THE MINIMUM SAMPLING PROGRAM, AND DIVERSITY MEASUREMENTS IN THE DRY ZONE, TRANSITION ZONE, AND *Scalesia* FOREST ON THE NORTH SIDE OF SANTA CRUZ

ZONE	DRY ZONE							TRANSITION ZONE				MOIST ZONE				
SAMPLE SITE NO.	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)
ALTITUDE (m)	90	150	210	250	290	350	390	420	470	500	540	570	590	600	630	640
*Croton scouleri** (narrow-leaved forms)	17	7	2	0	0	0	0	0	0	0	0	0	0	0	0	0
*Castela galapageia**	4	3	6	2	1	0	0	0	0	0	0	0	0	0	0	0
Acacia insulae-iacobi	4	6	1	6	1	0	0	0	0	0	0	0	0	0	0	0
*Gossypium barbadense**	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bursera graveolens	65	53	65	58	58	50	65	41	42	34	28	2	0	0	0	0
*Scalesia crockerii**	4	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Waltheria ovata	6	3	2	1	4	1	1	7	7	5	0	0	0	0	0	0
*Cordia anderssonii**	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	3
*Opuntia echios**	1	0	1	0	2	0	1	1	0	0	0	0	0	0	0	0
*Tournefortia pubescens**	0	2	2	5	0	5	0	3	2	4	1	0	0	0	0	0
Piscidia carthagensis	0	18	7	10	20	18	0	1	4	1	0	0	0	0	0	0
Chiococca alba	0	5	1	1	0	2	1	7	1	0	2	2	1	0	0	2
Scutia pauciflora	0	4	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Zanthoxylum fagara	0	1	8	15	14	13	3	16	8	6	12	23	2	7	7	1
Tournefortia psilostachya	0	0	1	0	0	0	0	0	1	2	2	0	0	0	0	0
Vallesia glabra	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
*Pisonia floribunda**	0	0	0	6	4	14	22	23	13	23	33	23	5	0	0	0
Erythrina velutina	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
*Psidium galapageium**	0	0	0	0	0	0	0	5	21	29	23	34	14	0	8	0
*Tournefortia rufo-sericea**	0	0	0	0	0	0	0	0	2	1	4	4	0	5	3	0
Maytenus octogona	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
*Scalesia pedunculata**	0	0	0	0	0	0	0	0	0	0	0	14	82	93	85	98
*Acnistus ellipticus**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Number of trees	105	103	102	104	105	104	94	105	101	105	106	104	104	105	105	104
Number of species	9	11	14	9	9	8	7	10	10	9	9	9	5	3	5	4
S_{50}	7.6	9.3	10.1	7.6	7.0	6.7	5.0	8.2	8.4	7.6	7.3	7.4	4.2	3.0	4.6	3.1
Fisher's α	2.4	3.1	4.4	2.4	2.4	2.0	1.8	2.7	2.8	2.4	2.4	2.4	1.1	0.6	1.1	0.8
Shannon's H'	1.9	2.4	2.1	2.1	2.0	2.2	1.3	2.5	2.5	2.4	2.4	2.4	1.0	0.6	1.0	0.4

NOTE: Asterisks indicate endemics.

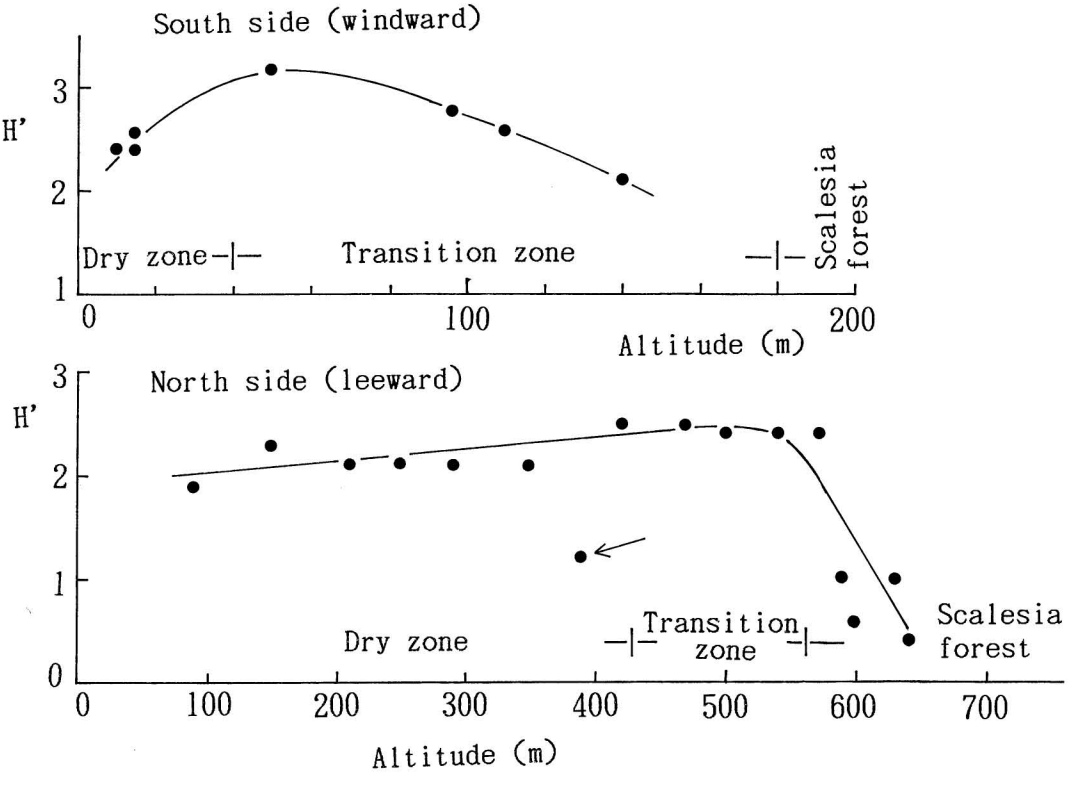

FIGURE 8. Patterns of diversity indices (Shannon's H' values) along the altitudinal gradient on the south and north sides of Santa Cruz. The arrow shows an exceptionally low value, caused by unresolved factors.

end of the transition zone, with an exceptionally low value at one site (near 400 m altitude). Reeder and Riechert (1975) reported a similar pattern on the southwest side of the same island. The H' values of the present study were low in the *Scalesia* forest. The pattern on the south side (Figure 8, top) departed from that on the north side, but gave similarly low H' values in the *Scalesia* forest (near 200 m on the windward and near 700 m on the leeward sides).

In the fertile moist zone, the species-poor constitution is related to the monodominance of *Scalesia pedunculata*. The monodominance of this species is one reason for the stand-level dieback (Itow and Mueller-Dombois 1988, Lawesson 1988). *Scalesia pedunculata* is very shade-intolerant, so seedlings and saplings are absent under mature forest canopy (Itow and Mueller-Dombois 1988). In the plant succession that takes place in the species-poor *Scalesia* forest belt, there are no tree species that precede *S. pedunculata*, and no tree species that succeed it. When *S. pudunculata* cohorts get old, the cohort members die more or less synchronously, resulting in a stand-level dieback. Such dieback appears to be an integral part in the dynamics of plant succession in this extremely species-poor forest of the Galápagos ecosystem, a phenomenon functionally comparable to the *Meterosideros* rainforest dieback in Hawaii (Mueller-Dombois 1983, 1987).

CONCLUSIONS

This paper focused on the vegetation structure by analyzing zonation-related trends and patterns in plant endemism, species turnover rate, and species diversity. The purpose was to compare these vegetation parameters on

the windward, wet south side with those on the leeward, dry north side of Isla Santa Cruz. Before the analyses, the upward deflection of vegetation zones on the north side was reconfirmed by studying plant distributions in an x–y dimensional space of elevation and substrate.

The trends of endemism across the zones were basically similar on the south and north sides. They displayed high endemism of woody species in the high-altitude zones while herbaceous plants showed opposite trends, at least on the south side. The overall turnover rate of species across the zones was three times greater on the windward south side (rate = −0.0039) than on the leeward north side (rate = −0.0013). The results coincide with the upward deflection of the vegetation zones on the north side. Diversity measurements on both sides were not even. A low diversity in the *Scalesia pedunculata* forest apparently resulted from the monodominance of this species. This may contribute to stand-level dieback as recorded there before. The parametric analysis and description of vegetation structure as presented here will open a way for comparative studies between floristically different islands.

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